ALPINE ANNUAL PLANT SPECIES IN THE WHITE MOUNTAINS OF EASTERN CALIFORNIA

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Abstract

The White Mountains resemble the Sierra Nevada in having an unusually high concentration of alpine annual plant species. Thirteen species of annuals comprise 8% of the alpine flora of the White Mountains. Most species (69%) have distributions that extend throughout western North America; however, they are known to occur above treeline only in the White Mountains and Sierra Nevada. Two of 13 species of alpine annuals in the White Mountains have distributions from near sea level to the alpine, three occur from the desert to the alpine, and seven have distributions from the coniferous forest to the alpine in California. Three additional species (*Chenopodium rubrum, Gentiana tenella,* and *G. prostrata*), generally known as annuals, function as biennials in alpine habitats of the White Mountains.

Few species of annual plants occur in alpine environments (Billings and Mooney 1968, Bliss 1971, Billings 1974). This probably reflects the inability of most annuals to successfully complete their life cycle in a short, cold growing season. The Sierra Nevada of California, however, has an unusually large number of annual plants at high elevations. Sharsmith (1940), for example, lists about 10 annuals in the alpine zone, and Went (1953) and Jackson (1985) describe approximately 47 annuals in the high subalpine and alpine zones.

The ability of annuals to occupy alpine habitats in the Sierra Nevada may be caused by relatively high levels of solar radiation and more moderate conditions (due to fewer summer storms) than are generally found in other alpine areas (Chabot and Billings 1972, Jackson 1985). An abundance of annual plant species at lower elevations, some of which may have been pre-adapted to conditions at higher elevations, contribute to the increased number of alpine annuals in the Sierra Nevada (Went 1953, Chabot and Billings 1972, Jackson 1985).

The alpine zone of the White Mountains is similar to the Sierra Nevada in having relatively warm dry summers with high levels of solar radiation and large numbers of annuals at lower elevations (Lloyd and Mitchell 1973, Major and Taylor 1977). On this basis,

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a relatively high concentration of annuals should occur at high elevations in the White Mountains. This study tests this prediction and provides information on the distribution of alpine annual plant species in the White Mountains of eastern California.

Study Area

The White Mountains are located in the eastern part of central California (37°13′–38°N and 117°55′–118°25′W), with the extreme northeastern portion extending into Nevada. The range is approximately 90 km long and 32 km wide at its widest point and is about 2278 km^2 in area. Because the Sierra Nevada occurs immediately to the west, the White Mountains are in a pronounced rain shadow and the vegetation is Great Basin in character (Lloyd and Mitchell 1973, Major and Taylor 1977). The four main plant zones described in Lloyd and Mitchell (1973) are desert scrub (1220–1980 m), pinyon woodland (1980–2895 m), subalpine forest (2895–3505 m), and alpine tundra (3505–4340 m). Within these vegetation zones, they list 811 taxa of vascular plants of which 20% (160 species) occur in the alpine zone. Recent collections have increased the total number of known species in the White Mountains to 988 (Morefield 1986).

Climatic records from 1953 through 1973 at the Barcroft Laboratory (elevation 3801 m) of the White Mountain Research Station indicate a mean July temperature of 7.4°C, a mean January temperature of −9.1°C, a mean annual temperature of −5.8°C, and a mean annual precipitation of 49.6 cm, of which 18.3% (9.1 cm) falls during June, July, and August (Pace et al. 1974).

Methods

The number and proportion of annual plant species in each of the four major plant zones of the White Mountains were based on species distributions given in Lloyd and Mitchell (1973). Life cycles for species not included in this flora were obtained from other floras (primarily Munz 1968, Hitchcock et al. 1969). Geographic affinities were categorized as cosmopolitan, western North American (widely distributed at low and high elevations from the Pacific Coast to the Rocky Mountains), and endemic (restricted to the White Mountains and nearby Sierra Nevada and Sweetwater ranges) according to descriptions in Munz (1968), Hitchcock et al. (1969), and Jackson (1985). Elevational distributions were based on Lloyd and Mitchell (1973) and Spira (pers. obs.) for the White Mountains and Munz (1968) for California. Field observations by the author were confined to the southern part of the range (south of White Mountain Peak).

Voucher specimens were deposited at JEPS. Nomenclature follows Lloyd and Mitchell (1973); for species not included in this source, nomenclature follows Munz (1968).

Results and Discussion

The number and proportion of annual plant species in each of the major plant zones of the White Mountains are shown in Fig. 1. Annuals become progressively less common with increasing elevation. For example, an analysis of species distributions as listed in Lloyd and Mitchell (1973) indicates that the desert scrub (the lowest zone) has 148 annuals (comprising 35% of the desert flora), whereas the alpine zone has only five annuals (comprising 3% of the alpine flora).

Field observations by the author from 1980–1985 revealed eight additional annuals in the alpine zone (Table 1). This increases the known number of alpine annuals to 13 species (8% of the alpine flora) in the White Mountains. Because annuals are easily overlooked due to their small size and short life cycle, further field studies would undoubtedly reveal additional species in each plant zone. Although the data shown in Fig. 1 underestimate the total number of annual plant species, they do indicate the relative number of annuals in each of the four major plant zones.

The 13 species of alpine annuals in the White Mountains represent 11 genera in 10 families (Table 1). This list is conservative in that it does not include species having an annual and/or biennial life cycle (discussed later) or species described as annuals to perennials (e.g., *Calyptridium umbellatum* var. *caudiferum, Androsace septentrionalis* ssp. *subumbellata*). Also, because my field observations were limited to alpine areas in the southern part of the range (south of White Mountain Peak), additional alpine annuals may occur in the northern part of the range.

Geographical distribution. Alpine annuals in the White Mountains generally have wide geographical distributions (Table 1). Nine of 13 species (69%) have a western North American distribution, two (15%) are weedy annuals with a cosmopolitan distribution, and only two species (15%) are endemic to the White Mountains and nearby Sierra Nevada-Sweetwater ranges.

None of the nine alpine annuals with a western North American distribution are known to occur in the alpine zone outside of the White Mountains and Sierra Nevada. The apparent ability of these nine species to occur at higher elevations in the White Mountains and Sierra Nevada relative to other mountain ranges could be explained by a warmer, drier growing season. In lower radiant energy areas, there may not be sufficient time for annuals to complete their life cycle and form viable seed, particularly in unusually short growing seasons (Jackson 1985).

Jackson (1985) lists the proportion of annuals at or above treeline in a number of western North American mountain ranges. Of the 19 areas sampled, seven (37%) had less than 1% annuals, nine (47%)

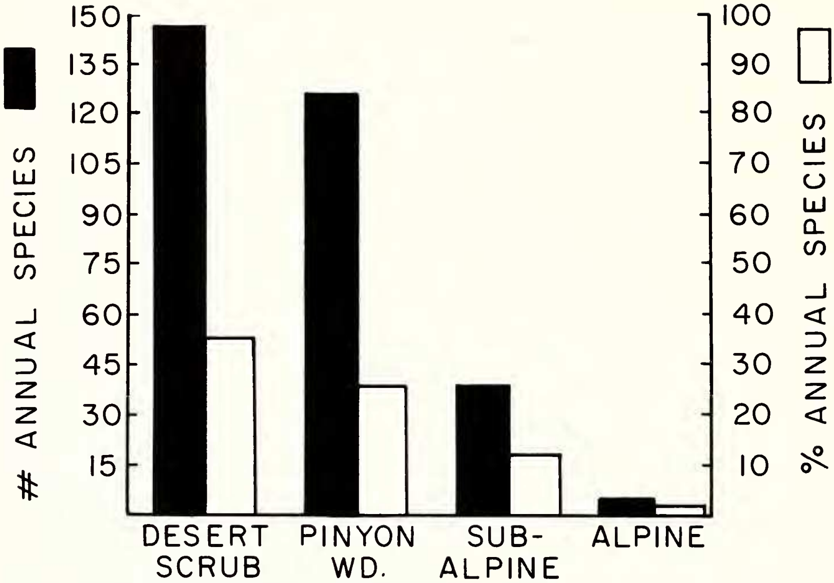

FIG. 1. Number of annual plant species and percent annuals within four main plant zones of the White Mountains based on Lloyd and Mitchell (1973). Recent field observations by author have increased the known number of alpine annuals in the White Mountains from 5 to 13 species (8% of alpine flora).

had 1–4% annuals, and only three (16%) had more than 4% annuals at or above treeline. The Wassuk Range, NV (4.3% annuals), Charleston Mountains, NV (7.6% annuals), and Hall Natural Area, Sierra Nevada, CA (8.3% annuals) comprise the latter group. The Wassuk Range and Charleston Mountains were based on samples of only 70 and 39 species, respectively. Consequently, more comprehensive surveys need to be made prior to evaluating these two areas.

The proportion of annuals in the alpine flora of the White Mountains was comparable to the Hall Natural Area of the Sierra Nevada, the area with the highest proportion of alpine annuals in Jackson's (1985) survey of western North American mountain ranges. Although annuals comprised about 8% of the alpine flora in both ranges, the number of alpine annuals in the Sierra Nevada was much greater than in the White Mountains (47 vs. 13 species). In addition to a larger pool of species, the Sierra Nevada survey included annuals in both the high subalpine and alpine zones (Jackson 1985), whereas only annuals known to occur above treeline were included in the present survey.

TABLE 1. SPECIES, FAMILY, AND GEOGRAPHIC AFFINITY OF ALPINE ANNUAL PLANT SPECIES IN THE WHITE MOUNTAINS. [1] = Species listed in alpine zone of the White Mountains by Lloyd and Mitchell (1973); [2] = Restricted to White Mountains and nearby Sierra Nevada and Sweetwater ranges; [3] = Extends into eastern North America as a weed.

Species	Family	Geographic affinity
Cryptantha glomeriflora[2]	Boraginaceae	Endemic
Mimulus coccineus[2]	Scrophulariaceae	Endemic
M. suksdorfii[1]	Scrophulariaceae	w. North American
Nama densum[1]	Hydrophyllaceae	w. North American
Juncus bryoides	Juncaceae	w. North American
Gayophytum racemosum	Onagraceae	w. North American
Gymnosteris parvula[1]	Polemoniaceae	w. North American
Eriogonum cernuum[1]	Polygonaceae	w. North American
Calyptridium roseum[1]	Portulacaceae	w. North American
Chenopodium atrovirens	Chenopodiaceae	w. North American
C. leptophyllum[3]	Chenopodiaceae	w. North American
Monolepis nuttalliana	Chenopodiaceae	Cosmopolitan
Capsella bursa-pastoris	Brassicaceae	Cosmopolitan

Elevational distribution. Upper elevational extremes for alpine annuals in the White Mountains (Table 2) were consistently higher than those listed by Munz (1968) for California. Because elevational distributions in large floras are not always reliable, it is unclear whether or not alpine annuals in the White Mountains occur at higher elevations than elsewhere in California.

In the White Mountains, however, alpine annuals generally have broad elevational distributions (Table 2). Ten of the 13 species (77%) occur at elevations ranging from less than 1850 m to more than 3500 m. Within California, two of the 13 species (*Capsella bursa-pastoris* and *Monolepis nuttalliana*; 15%) have distributions from near sea level to the alpine, three species (23%) occur from the sagebrush (desert) scrub to the alpine, and seven species (54%) have distributions from the coniferous forest to the alpine (Table 2).

Jackson (1985) found that alpine annuals in the Sierra Nevada also have broad elevational ranges and suggests they migrated to higher elevations from lower elevation populations. Went (1948) and Chabot and Billings (1972) also suggest a low elevation origin for Sierran alpine annuals and note that conditions in the alpine in July and August are similar to those at lower elevations in March and April (e.g., high light levels, large diurnal temperature fluctuations, and limited moisture availability). Consequently, lower elevation annuals may have been pre-adapted, at least to some extent, to an alpine environment.

Axelrod (1981) suggests that a warmer, drier climate in the xe-

TABLE 2. PLANT COMMUNITY AND ELEVATIONAL RANGE OF ALPINE ANNUALS IN CALIFORNIA (MUNZ 1968) AND UPPER ELEVATIONAL EXTREME IN WHITE MOUNTAINS (LLOYD AND MITCHELL 1973 AND THIS STUDY). * = J. Morefield, pers. comm. ** = Not available.

Species	Plant community	Elevation (m)		Highest elevation (m) in White Mtns.
		Low	High	
Nama densum	sagebrush scrub to lodgepole forest	910	3570	3570
Calyptridium roseum	sagebrush scrub to lodgepole forest	1520	3200	3750
Chenopodium leptophyllum	sagebrush scrub to yellow pine forest	1520	2440	3750
Chenopodium atrovirens	pinyon juniper wd. to red fir forest	1220	3350	3780
Eriogonum cernuum	**	2130	3050	3200
Juncus bryoides	montane coniferous forest	1280	3350	3660
Gayophytum racemosum	montane coniferous forest	1520	3350	3970*
Mimulus suksdorfii	montane coniferous forest to alpine	1520	3960	4050
Cryptantha glomeriflora	montane coniferous forest	1830	3350	3750
Gymnosteris parvula	bristle-cone pine forest	2530	3600	3830*
Mimulus coccineus	lodgepole pine forest to alpine	2440	3660	3980
Monolepis nuttalliana	many communities	**	2740	3970*
Capsella bursa-pastoris	many communities	**	2130	3540

rothermic (ca. 8000–4000 yr B.P.) facilitated species migrations from lower to higher elevations in the Sierra Nevada (and presumably in the White Mountains). Thus, a number of annuals may have migrated successfully into the alpine zone at this time. As temperatures dropped and rainfall increased following the xerothermic, some annuals probably were eliminated, whereas others may have persisted in favorable microsites at high elevations.

Went (1948) and Chabot and Billings (1972) suggest that nearby deserts were the primary source of alpine annuals in the Sierra Nevada. In a recent floristic study, Jackson (1985) suggests that montane coniferous forests were probably the primary source of alpine annuals in the Sierra Nevada. Because 23% of alpine annuals in the White Mountains extend from the sagebrush (desert) scrub to the alpine and 54% extend from the coniferous forest to the alpine, both the desert and forest were probably important source areas for alpine annuals in the White Mountains.

Habitats. The alpine annuals observed in this study were almost always found on bare soil, and often on dry south-facing slopes. The high light levels, comparatively warm temperatures, and reduced competition for soil moisture in such habitats enhance the ability of annuals to successfully complete their life cycle in a short growing season (Jackson and Bliss 1982).

Alpine annuals were observed frequently along roadsides and grazed areas in the White Mountains, which suggests humans and domestic animals (e.g., sheep and cattle) have increased available habitat and may have introduced seeds of some annuals into the alpine zone. This was probably the case for six weedy annuals restricted to a disturbed roadside area immediately south of the entrance gate to the Barcroft Laboratory, where cars occasionally parked and where horses were tethered during the fall hunting season. Because populations of five of these species (*Sisymbrium irio, S. orientale, Descurainia sophia, Stellaria media,* and *Senecio vulgaris*) were small (generally fewer than 10 plants), highly localized, and present in only one or at most two of the six years (1980–1985) observations were made, they were not included in my list of alpine annuals in the White Mountains.

Capsella bursa-pastoris was a sixth weedy annual restricted to the same roadside area. Unlike the other five species, however, a stable population of 25 to several hundred individuals was maintained during five successive years, and the area occupied by this species increased during the period of study. Thus, *C. bursa-pastoris* appears to have successfully colonized the alpine zone; but it and several other weedy alpine annuals (e.g., *Monolepis nuttalliana, Chenopodium atrovirens,* and *C. leptophyllum*) probably would not be present, or would be much less common in the alpine zone of the White Mountains, were it not for the presence of disturbed areas.

Life cycle variation. Except for *Nama densum* and *Eriogonum cernuum,* I observed each of the 13 alpine annuals described here under field conditions. As expected, individuals of each species germinated, flowered, fruited, and died within a single summer. In contrast, several other species, generally described as annuals, exhibited a biennial life cycle in alpine habitats of the White Mountains. For example, *Gentiana tenella* is described as an annual and *G. prostrata* as an annual and/or biennial in regional floras (e.g., Abrams and Ferris 1960, Munz 1968, Hitchcock et al. 1969). In the White Mountains, however, individuals of both species consistently form a vegetative rosette during their first summer, overwinter as a taproot, and then flower, fruit, and senesce during their second summer. Unlike a number of purported biennials in which plant size (rather than age) determines when flowering occurs (Gross 1981), individuals of *G. tenella* and *G. prostrata* flowered in their second year regardless of plant size (Spira 1983).

Chenopodium rubrum is known as an annual that occurs at elevations to 1000 m in Britain, 2000 m in the European Alps, and 3000 m in the United States (Williams 1969). In the White Mountains, however, I have observed *C. rubrum* in alpine habitats to 3750 m, where individuals grow vegetatively one summer and then flower, fruit, and die during their second summer.

A biennial rather than annual life cycle in alpine individuals of *C. rubrum* may be influenced by several factors. First year plants may fail to reach some critical size before flowering can be induced, individuals may require a cold treatment (as overwintering plants would receive) prior to flowering, or individuals may not receive the necessary photoperiod to induce flowering during their first summer's growth (Harper 1977). It would be interesting to know whether the shift in life cycle in *C. rubrum* is a genotypic response (i.e., life cycle ecotypes over an elevational gradient) or an environmentally controlled (phenotypic) response, and at what elevation the shift from an annual to a biennial life cycle occurs.

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